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Early Human-Bison Population Interdependence in the Plains Ecosystem

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EARLY HUMAN-BISON POPULATION INTERDEPENDENCE IN THE PLAINS ECOSYSTEM

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ABSTRACT—Human population size in the Great Plains ecosystem before European contact has been of longstanding interest to scholars. The same is true of bison numbers. Given the near total dependence on bison by nonagricultural precontact humans, integrating information on both human and bison numbers from that time is of further interest, providing the focus for this paper. Recent research on the behavioral ecology of bison and related ungulates has led to the identification of two distinct, although not mutually exclusive, populations: resident and migrant herds. Moreover, migrants tend to vastly outnumber residents, often by more than 4 to 1. The best available evidence supports estimates of about 30 million bison in the Plains ecosystem during prehistoric and early historic times. Of these, about 6 million likely were nonmigrants at any one time. These numbers provide a basis for estimating the numbers of human bison-hunters. We review four possible combinations of human use of resident and migratory bison populations and their implications for human numbers. Archaeological and historical information provides evidence that year-round use of residents, together with seasonal use of the more numerous migrants, was the most likely pattern of human usage of bison. Hence, we estimate the sustainable human bison-hunting population to have been 86,000-130,000. This estimate is close to past population estimates based on direct counts and other extrapolations.

Introduction

Early records and archaeological data show that bison once existed throughout the North American Great Plains and that nonagricultural aboriginal people were dependent on the bison as their principal means of

subsistence (Roe 1970; Dyck 1983; Bamforth 1988; Dyck and Morlan 1995). Estimates of early historic Plains bison populations often have been high, up to 40 million animals at any one time (e.g., Roe 1970). At the same time, estimates of early historic human populations of Plains bison-hunters have tended to be relatively low, in the range of 100,000-200,000, except for several much higher estimates that are meant to compensate for postulated effects of European diseases (e.g., Mooney 1928; Dobyns 1983; Ramenofsky 1987; Ubelaker 1988; Campbell 1989; Daniels 1992; Owsley 1992; Thornton 1997).

Our goal is to deduce human population potential in relation to bison population estimates in the Plains ecosystem during late prehistoric and early historic times, and to relate this potential to previous human population estimates. We draw on information available pertaining to bison behavioral ecology and human settlement patterns, and integrate these data to address this goal. Our geographic emphasis is on the Great Plains grasslands and adjacent woodlands, the Plains ecosystem, in which the bison was the keystone herbivore during the time in question (Coupland and Brayshaw 1953; Roe 1970; Meyer and Epp 1990).

Like other nonterritorial migrant ungulates (Estes 1974), bison tend to have two distinct populations, a resident and a migratory group (e.g. Soper 1941; Stelfox et al. 1986). Migrants tend to far outnumber residents, often by 4 to 1 or more (Soper 1941; Fryxell et al. 1988). Given the potential human-bison population relationships, we ask: How did the dual dispersion strategy of bison affect human demographics and population limits? Also, were human numbers dependent on the migrant bison, the resident herds, or both?

First we examine recent research on ungulate behavioral ecology and its implications for bison movements and numbers. Then, we pose four trial cases of human-bison numbers relationships and test them against new information on bison populations, factoring in what is now known about their dual dispersion strategy. Finally, we compare the results of the tests to other estimates of Plains bison-hunter populations.

Methods

Time and Place

We restrict temporal perspective to the last 5,000 years. The open Plains are a relatively recent phenomenon (Owen-Smith 1987), and so are the vast herds of bison that occupied them until the late 19th century (Wyckoff and Dalquest 1997).

During this time interval, the main range of the North American bison was the Plains ecosystem, although smaller populations occurred in grassy meadows in the eastern forest and in the western boreal forest (Roe 1970). Historical information shows that the migrant bison herds spent the summer in open grasslands and the winter in wooded valleys and hills, or in the lightly wooded to grassy transition zones between open grasslands and adjacent forests, although movements often were irregular (Roe 1970; Morgan 1980; Malainey and Sherriff 1996). Resident herds likely occupied the lightly wooded valleys, hills, and transition zones the year round (Epp 1988).

Consideration of bison and human population density in the Plains ecosystem requires an estimate of the total area. We accept Isenberg's (2000) recent indirect estimate of the area as just over 3.1 million km^2.

Influence of Migration on Bison Populations

Bison numbers in the Plains ecosystem have been subject to much speculation and investigation (e.g., Roe 1970; McHugh 1972). Unfortunately, scientific investigations did not begin until bison numbers had been greatly reduced, making early historic population estimates difficult to verify. Recent estimators (e.g., Isenberg 2000) use a combination of historic information and contemporary wildlife science.

Bison migration has received similar attention (e.g., Roe 1970; McHugh 1972; Morgan 1980; Hart 2001). Research on ungulate behavioral ecology has shown that migration and numbers of individuals can be closely related (e.g., Fryxell, et al. 1988). We accept Baker's (1978) definition of "return migration," somewhat irregular yet identifiable travel between different spatial units, as applicable to bison movements.

Research on mobility of nonterritorial ungulates, including bison, has provided three bases for a reassessment of bison numbers and population dynamics: (1) there are often two discrete populations of a species within any given area at any one time; (2) one of these populations migrates between two distinct home ranges; and (3) migrants tend to have larger home ranges and to vastly outnumber residents (e.g., Soper 1941; Stelfox et al. 1986; Crete and Huot 1993). The movement is possible because these animals do not defend territories, being continually mobile, although the individual herds do have home ranges (Kelsall 1968; Estes 1974; Fryxell et al. 1988). This information has profound implications for estimating dependent human populations.

The population disparity is true also for East African plains zebra and wildebeest and North American caribou, although their movements tend to

be more regular than do those of bison (Fryxell et al. 1988; Crete and Huot 1993). A range in the proportion migrating has been observed from 40% in plains zebra, to 90% and higher in wildebeest, to 98% in Quebec caribou (Stelfox et al. 1986; Crete and Huot 1993). Also important is the observation that the proportion of migrant animals tends to increase as the overall population grows (Stelfox et al. 1986). Soper (1941) identified a difference of 4 to 1 migrants to residents among bison in Wood Buffalo National Park. In the past, disparities likely were higher during productive years, but it seems reasonable to ascribe a conservative migrant-to-resident population relationship of 4 to 1 for Plains ecosystem bison as normal, and that is what we use as the basis of our estimates.

Evidence suggests strongly that the disparity between migrant and resident ungulate numbers is caused by the act of migration. Tests performed by Fryxell et al. (1988) in East Africa have shown that the main advantage of migration is that it reduces predation significantly. This is because most predators of ungulates are territorial. They are tied to specific confined spaces within an ecosystem, either permanently or during the crucial time of year when they have their young, and are unable to follow the migrants when these leave the habitat for half of each year (Parker 1973; Fryxell et al. 1988). Migrants' ability to reduce predation overrides the effects of disease and accidents to the point where food supply becomes the main limiting factor (Fryxell et al. 1988; Sinclair and Arcese 1995). Thus, predators of ungulates can limit only the populations of resident prey (Fryxell et al. 1988). Alternatively, such a situation prevents predators from attaining numbers near to their biological potential.

What were the predators of late prehistoric bison in the Plains ecosystem? Other than humans, there were the wolf, coyote, grizzly bear, and cougar (Roe 1970; Krech 1999). Of these, grizzlies and cougars defend year-round territories, and the canids, wolves and coyotes, defend territories during the denning season but move around larger home ranges during the rest of the year (Parker 1973; Banfield 1974). Among nonhumans, wolves have been the main predator of bison over the past 10,000 years (Lott 1991; Krech 1999).

In contemporary East Africa the main predators of grazing ungulates (lions and hyenas) are territorial, unable to follow migrant prey (Fryxell et al. 1988). The migrant wildebeest move between disparate home ranges as did bison during the time in question, but with more regularity than did bison (Stelfox, et al. 1986). Specifically, in the Serengeti-Mara ecosystem, where migration is important, annual predation on wildebeest is only 1%,

but resident wildebeest in the Ngorongoro area suffer a 10% annual loss to predation, which limits population size (Fryxell et al. 1988). The reproductive rates of both wildebeest and bison are alike, normally one birth per female per year (Roe 1970; Estes 1974). Fryxell et al. (1988) have concluded, on the basis of such observations, that populations of resident ungulate grazers are unlikely to stabilize at high densities in home ranges that overlap with large migrant populations.

The implications of wildebeest and caribou migrations to the populations of Plains bison are clear. Movement of bison over more than one home range similarly removed the restrictions to population increase inherent in resident herds. Given the different environments and species involved, however, bison movements were less predictable (Roe 1970; McHugh 1972; Hart 2001). There are further implications. First, predators of bison likely were not as effective in dispatching their prey as are predators of wildebeest. Lions and hyenas are considerably larger than wolves, and bison are larger than wildebeest (Macdonald 1984). Second, grizzly bears are primarily vegetarian (Banfield 1974; Lott 1991), although bison calves likely were taken occasionally. Killing a fully grown bison would have been beyond the normal capabilities of cougars (Lott 1991). Furthermore, as both grizzlies and cougars defend territories (Banfield 1974), no individual would have been able to prey on migrant bison once the herds had vacated its territory. Wolves likely preyed on bison calves in the spring, whenever these were available within their denning territories, but bison adults are remarkably effective at protecting their calves against wolves (Carbyn and Trottier 1988). Thus, wolves likely had little effect on the overall bison population and its reproductive potential, and coyotes had even less effect (Banfield 1974; Lott 1991). Compared to wildebeest, the overall animal predation rate on bison likely was low as well, no more than 1% per year for the migrant population. Given these conditions, we estimate conservatively, that the annual predation rate on resident bison must have been about one-half that on resident wildebeest, or 5%. An important implication for human bison-hunters, then, is that very large numbers of bison were available each year for sustainable use.

Previous Human Population Estimates

What were the previous estimates of prehistoric and early historic human bison-hunters in the Plains ecosystem? We draw from a variety of estimates, even though they are not consistent in area covered (Table 1). For

TABLE 1

PREVIOUS ESTIMATES OF TOTAL GREAT PLAINS HUMAN POPULATION SIZE

Date (AD)	Population	People per km^2	Source
1500	189,100	0.06	Ubelaker 1988
1520	1,333,000[a]	0.43	Dobyns 1983
1600	89,100	0.03	Ubelaker 1988
1690-1780	142,000	0.04	Mooney 1928
1700-1811	138,250+	0.04	Roe 1970
1700	89,100	0.03	Ubelaker 1988
1800	120,330	0.04	Ubelaker 1988
1850	103,136	0.03	Ubelaker 1988
1900	62,656	0.02	Ubelaker 1988
1907	53,000	0.01	Mooney 1928

[a]Minimum

the time frame considered here, we draw a distinction between two human subsistence types in late prehistoric times: bison-hunters dispersed throughout the Plains, and village agriculturalists along the eastern edge and the Missouri River (Isenberg 2000). Another important factor in human population estimates is the introduction of Old World diseases (e.g., Dobyns 1983; Romaniuc 2000) (Tables 1, 2).

Among the studies referring to the Great Plains as an areal unit (Table 1), Mooney's (1928) estimate of 142,000 people during the period AD 1690-1780 is key. This earliest enumeration is derived from historic and ethnological literatures. Once considered far too high, Mooney's (1928) estimates today are comparatively low. In contrast, the numbers provided by Dobyns (1983), based on subsequent disease-caused depopulation, are much higher. The specific value shown of about 1.3 million people (Table 1), is the closest we are able to come to a Plains estimate from Dobyns's (1983) work. Ubelaker's (1988) estimate is between Mooney's (1928) and Dobyns's (1983) estimates. It is based on a new compilation derived from an early version of the *Handbook of North American Indians* (2001).

Human population estimates for various portions of the Plains ecosystem provide insight into regional variations, including the influence of agricultural populations on overall population estimates (Table 2). For the

TABLE 2

ESTIMATES OF GREAT PLAINS HUMAN POPULATION BY AREA

Effective date (AD)	Area	Population density	Estimate/km^2	Source
1780	Northern Plains	28,700	0.05	Wissler 1936
1780	British Plains	21,500	0.05	Decker 1991
1780	Northern Plains	100,800	0.06	Mooney 1928
1790	Northern Plains	41,000	0.038	Kroeber 1939
1780	Northern Prairie	13,000	0.038	Kroeber 1939
1780	Village Prairie	9,000	0.15	Kroeber 1939
1780	Central Prairie	15,000	0.05	Kroeber 1939
1780	Middle Platte	10,000	0.076	Kroeber 1939
1780	Southern Prairie	16,000	0.034	Kroeber 1939
1780	Southern Plains	9,500	0.031	Kroeber 1939
1780	Red River	16,000	0.05	Kroeber 1939
1805	Northern Plains[a]	50,700+	0.03+	Moulton 1987[b]
1805	Northern Plains[c]	35,060+	0.02+	Moulton 1987[b]
1805	Northern Plains[a]	65,000+	0.04	Moulton 1987[d]
1809	Northern Plains	16,360	0.03	Wissler 1936
1843	British Plains	23,400	0.05	Lefroy 1853
1858	Northern Plains	25,620	0.05	Wissler 1936
1882	Northern Plains	24,291	0.04	Wissler 1936
1899	Northern Plains	15,434	0.03	Wissler 1936
1907	Northern Plains	50,477	0.03	Mooney 1928
1690	Southern Plains	41,000	0.03	Mooney 1928
1907	Southern Plains	2,861	0.002	Mooney 1928

[a]Maximum
[b]Without Blackfoot and Assiniboine
[c]Minimum
[d]Extrapolated, with 15,000 added for Blackfoot and Assiniboine

area referred to as the British (now Canadian) Plains, we calculated densities using an area of 450,000 km^2, following Horton (1994). Note that densities are more uniform than absolute population estimates for these Northern Plains, the result of different estimators delineating the region differently (e.g., Mooney 1928; Decker 1991). Where density figures were not provided already for the British Plains, we calculated them using the absolute numbers and the area described by the estimator. Kroeber's (1939)

estimates for the Plains were more detailed than others and showed significantly higher population densities, using the absolute numbers and agricultural areas, than those in zones dominated by bison-hunters (Table 2).

Bison Numbers and Human Use

What are the implications of migration research on estimates of bison numbers prior to their near extermination? For years, an aggregate total of 60 million animals, with 40 million in the Plains ecosystem, was the best number available (Seton 1910; Roe 1970). Newer estimates tend to be somewhat lower. For example, Krech (1999) accepts an estimate of about 30 million animals at any one time for the Plains area. His reasons for the lower estimates are: (1) a greater appreciation for the uneven distribution of bison over their range, and (2) the effects of drought.

Other, much lower late prehistoric bison numbers have been proposed as well, as low as 5-10 million animals (e.g., Kay 1996). Such estimates assume very high human numbers based on evidence of heavy use of other resources, creating a strong potential for bison overkill. These estimates are not consistent, however, with the effects of migrant behavior on bison populations, or with relevant archeological data that show an overwhelming reliance on bison by the nonagricultural human population (e.g., Bamforth 1988; Epp 1988; Frison 1991; Dyck and Morlan 1995). We accept Krech's (1999) bison population estimate of 30 million as reasonable for the time and place we address.

The number of animals required per individual per year is important in estimating human use of bison. Based on average animal weights and human consumption requirements, Krech (1999) calculated that one person would have required 6 bison per year, which is close to Isenberg's (2000) estimate. Yet the actual kill estimate must be somewhat higher due to some wastage (Krech 1999; Isenberg 2000). A waste allowance of one bison per person per year seems reasonable, bringing the kill estimate to 7 animals per person per year.

Results

Availability of Bison for Human Hunters

Given a total Plains population of about 30 million bison, at 80% the migrants would have numbered about 24 million at any one time, and the

residents about 6 million. Conservative animal predation rates of 1% for migrants and 5% for nonmigrants would result in the annual deaths of 240,000 and 300,000 bison respectively. These differential predation rates would have resulted in an overall annual predation rate of around 1.8%, or 540,000 animals. We can now apply our human kill rate of 7 bison per person per year to the proportion of the bison population available in order to estimate the human bison-hunter population for the time and place considered here.

New Human Population Estimates

How many bison would have been available to human bison-hunters in the Plains ecosystem during any nondrought year, given the information and calculations presented here? What would the implications have been for this human population? We examine four scenarios along a continuum of human usage in order to address these questions. These are: (1) continuous use of the total bison population; (2) use of migrant bison only; (3) use of resident populations only; and (4) continuous use of resident populations with seasonal use of migrants. These alternatives provide a range of potential human use and subsequent influence on human population size (Table 3).

(1) *Use of total bison population, continuously available.* Assuming a total population of 30 million animals during any given productive year, an animal predation rate of 1.8%, and a sustainability threshold for all predation of 10%, the sustainable kill for humans would be 8.2%, or roughly 2.5 million bison. Given an average annual kill of 7 animals per person, the maximum human bison-hunter population that could be sustained would be approximately 360,000 people.

(2) *Use of migrant bison only, continuously available.* Assuming a migrant bison population of 24 million during productive years, an animal predation of rate 1%, and a potentially sustainable predation rate of 10%, a bison population of 9%, or roughly 2.2 million animals, would be available for human hunters each year on a sustainable basis. Given an average annual kill of 7 animals per person, the maximum human bison-hunter population that could be sustained would be about 315,000 people.

TABLE 3

PLAINS ECOSYSTEM HUMAN BISON-HUNTER POPULATION ESTIMATES BASED ON CONSUMPTION OF SUSTAINABLE YIELDS OF BISON

Resource use	Estimated human population	Number of people per km^2
Full use of total bison population	360,000	0.11
Migrant bison only	315,000	0.10
Resident bison only	43,000	0.01
Residents plus seasonal use of migrant bison	86,000 to 130,000	0.02 to 0.04

(3) *Use of resident bison only, continuously available.* Assuming a population of 6 million resident bison, an animal predation rate of 5%, and a potentially sustainable rate of 10%, 5% of the resident bison, or about 300,000 animals, would be available for human use annually. Again, given an average annual kill of 7 animals per person, from this number of available bison we infer a sustainable human bison-hunter population of around 43,000 people.

(4) *Continuous use of resident bison and seasonal use of migrants.* Assuming a total bison population of 30 million during productive years, consisting of 24 million migrants and 6 million residents, availability of bison resources would have been about double to triple that of reliance on residents alone, given seasonal mass kills, mostly in fall and winter, and an average annual kill of 7 animals per person. This would have allowed a human bison-hunter population in the Plains ecosystem of about 86,000-130,000 people.

Discussion

How do these estimates compare with previous ones? First, scenarios 1 and 2, based on utilization of the entire bison population or on use of the whole migrant population, are similar only to previous estimates for areas in

which agriculture was important (Table 2). However, agriculture was not a consideration in our estimation process. Moreover, estimates in scenarios 1 and 2 are high because they assume levels of access to bison that seem impossible in practical terms. Historical records indicate that people simply were not able to fully synchronize their movements with those of the bison, and did not attain the maximum sustainable level of use until adoption of the horse culture (Isenberg 2000). Thus, neither historical records nor previous human population estimates are consistent with our first two possible scenarios.

Our third estimate, based on use solely of resident bison populations, is comparable to estimates of the Plains aboriginal population after the demise of the bison (e.g., Mooney 1928). These numbers are supported by historical observations that indicate frequent uncertainty about bison availability, which is inconsistent with sole reliance on resident herds. Also, they are well below other population estimates for the period before the bison extirpation (e.g., Mooney 1928). Thus, neither historical records nor previous human population estimates are consistent with this scenario as well.

This leaves our fourth scenario, based on a combined use of resident herds with seasonal access to migrants. The closest comparisons with most previous estimates are found here. All of the earlier historical estimates, except that of Dobyns (1983), are within a range of 0.03-0.06 persons per km^2 in the Plains ecosystem, bison-hunting and agricultural populations combined. In order for Dobyns's (1983) projected number of about 1.3 million persons to have survived while dependent on bison for subsistence, a population of at least 110 million bison would have been required. Consequently, we regard Dobyns's (1983) estimate as being too high. The other estimates, referring to times after the arrival of Europeans but before the precipitous decline of bison populations during the late 19th century, are uniformly within the range of 0.03 to 0.06 persons per km^2. If one regards the higher part of this range as reflecting the inclusion of denser pockets of Plains agricultural populations, then the density of mainly bison-hunting populations likely falls within the range of 0.03-0.04 persons per km^2. Hence, our fourth estimate is most comparable to previous credible estimates of early bison-hunting populations in the Plains ecosystem. Also, the idea that human populations subsisted by hunting both resident and migrant bison herds is consistent with historical perceptions of resource uncertainty (Roe 1970). Thus, comparisons with previous estimates and consideration of historical bison hunting conditions suggest our fourth estimate to be the most accurate.

If our fourth estimate is closest to reality, then the Plains bison-hunter population was well below the level that was potentially sustainable by the overall abundance of bison resources. The total human population estimate is numerically above the limited potential associated with resident herds, yet nowhere near the maximum potential associated with migrant herds.

Archaeological investigations support this intermediate level of human population. Data indicate that bison kills and habitation sites tend to be concentrated near areas of vegetation diversity and relatively high topographic relief near permanent water supplies (e.g., Adams 1976; Epp 1986; Frison 1991; Buehler 1997). Resident bison herds tended to have their home ranges in such areas, but these also overlapped with the home ranges of some of the migrants, causing intermingling of herds (Epp 1988). Such places had the variety of forage and shelter needed by residents year-round and by migrants seasonally (Epp 1988). Large open areas tended to be grazed heavily during the summers by the more mobile herds and then abandoned by them, but not regularly (Roe 1970; Epp 1988). Hence, we conclude that the lightly wooded environments were favored for habitation by the human bison-hunters in the Plains ecosystem since they provided ready access to both resident and migrant bison herds.

The expectation of reliable access to resident bison herds, with less certain seasonal access to large numbers of migrants, would have had two important effects on both the human and bison populations. It would have served to ease pressure on the resident bison and to allow a higher sustainable human population than would have been possible given access only to resident animals. Also, it would have provided an enormous source of food and other resources on occasion, which could be preserved to supply the needs of a human band for some time. Our results, then, support previous human population estimates based on historical compilations and provide an explanation for lower-than-expected estimates based on the total bison population.

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